A whole-ecosystem, long-term wetland experiment illustrates effects of macrophyte community diversity on ecosystem function

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Abstract

Our whole-ecosystem wetland experiment illustrates the role of introduced biodiversity on ecosystem function and the long-term effect of propagule introduction on ecosystem function in created and restored wetlands. Two 1-ha wetland basins with identical hydrology have been maintained for 6 years as part of a long-term, whole-ecosystem experiment on wetland ecosystem development. One basin was planted with macrophytes; both basins were then subjected to identical hydrologic conditions and natural colonization of plants, algae, microbes, and animals for 6 years. By the third year, the basins converged in function and remained so generally through the fifth year. By the sixth year of the experiment, the basins diverged in macrophyte cover diversity, with the planted basin maintaining a diverse plant cover dominated by several plant communities while the unplanted basin became dominated by *Typha* spp. This difference, in turn, caused a divergence in ecosystem function in the sixth year with differences in net primary productivity of macrophytes, water chemistry, benthic invertebrate diversity, and bird and other animal use. The study suggests that ecosystem energy flow affects biodiversity, not the other way around. Introducing propagules may enhance biodiversity of created ecosystems but not necessarily biological productivity or diversity of other parts of the ecosystem.

Introduction

There is great interest in ecology on the importance of biodiversity on ecosystem function. There are two schools of thought on this connection (Wardle et al., 2000). One group uses experimental approaches, often in replicated terrestrial plots with diversity of plants controlled and functions such as net primary productivity measured to connect cause and effect (Naeem et al., 1994; Tilman et al., 1996, 1997; Naeem and Li, 1997). A second group argues that ecosystem function is driven, not necessarily by species diversity but by dominant species present (Grime, 1997; Levine, 2000). That group has been criticized for relying on observational studies and not experimental studies (Wardle et al., 2000). Except for some studies of diversity and function in natural ecosystems, researchers have relied on artificially maintaining biodiversity and then measuring ecosystem functions and attributing the differing functions to those differences in biodiversity.

What we have here is a whole-ecosystem, large-scale, long-time, wetland experiment on biodiversity and its effect on ecosystem function. Whole-ecosystem experiments, which have been carried out for terrestrial systems (Likens, 1977; Sullivan, 1993; Beier and Rasmussen, 1994), aquatic systems (Schindler, 1977; Schindler et al., 1997), and wetlands (Odum et al., 1975; Mitsch et al., 1995, 1998) can be less stochastic and thus more homeostatic, and often allow for the demonstration of ecosystem properties that otherwise would not appear in smaller scale experiments (Pomeroy et al., 1988; Odum, 1990, 1992; Beyers and Odum, 1993; Carpenter et al., 1995; Carpenter, 1998). We believe that estimating the effects of biodiversity on ecosystem function can best be seen at large-scale experiments that cover enough area for full ecosystem development to occur and occur over a time long enough for changes to mainfest themselves. Ecosystem functional differences cannot be predicted in elegant short-term, replicated small plots or mesocosms that represent only a part of an ecosystem and that are not allowed to receive major infusions of propagules during the experiment. After several years of converging function, one of our created wetland basins developed a diversity of emergent plant

communities while the other developed a monoculture of emergent vegetation. We thus have an ideal situtation in this sixth year of wetland development in the two basins to determine if the different biodiversity in the wetlands causes differences in ecosystem function or if it is insensitive to this plant diversity. Our wetlands were allowed to establish naturally through self-design (Mitsch, 1995,1996; Mitsch and Wilson, 1996; Metzker and Mitsch, 1997; Mitsch et al., 1998) with no human intervention in the two basins except the original introduction of plants to one basin in 1994.

What we also have here is a long-term experiment on wetland creation, specifically started to investigate the importance of propagule introduction on ecosystem function and diversity and to determine if and when planted and unplanted basins will diverge and/or converge in ecosystem function. Our hypothesis is that "planted and unplanted wetlands will be similar in function in the beginning, diverge in function during the middle years, and ultimately converge in structure and function." There is much interest in the question of whether introducing propagules, particularly plants, has any measurable effect on ecosystem function in the creation and restoration of wetlands (Streever and Zedler, 2000; Mitsch et al., 2000). There is also controversy over whether we can create or restore wetlands for habitat support at all (Roberts, 1993; Zedler, 1996; Young, 1996; Hammer, 1997; Mitsch et al., 1998; Malakoff, 1998; Mitsch and Gosselink, 2000). Our whole-ecosystem experiment (Mitsch and Wilson, 1996; Mitsch et al., 1998) was designed to determine the importance of human introduction of organism propagules on long-term ecosystem function of created wetlands.

Methods

Two 1-ha experimental wetlands and a river water delivery system were constructed at The Olentangy River Wetland Research Park (Figure 1), a 10-ha site on the campus of The Ohio State University in Columbus. Over 2,400 plant propagules (mostly root stock and rhizomes) representing 13 species typical of Midwestern USA marshes were planted in one wetland (Wetland 1=W1) in May 1994. Wetland 2 (W2) remained unplanted. Both wetlands have received the same amount and quality of pumped river water for six years and both have had essentially identical hydroperiods for the entire study period (Figure 2). Pumped river water generally flows into the wetlands continuously, day and night except for winter months, planned drawdowns, and periods of pump failure. After start-up trials in 1994, a pumping protocol was developed that involves changing the pumping rate manually 2 or 3 times a week according to a formula that allows more pumping when river discharge is high and less pumping when river flow is low. On an annual average, pumped inflow has been 20-40 m/yr. Water depths in the major portions of the wetland are generally 20 to 40 cm in the shallow areas and 60 to 100 cm in the deepwater areas. Five flooding events occurred during the period of 1995-96. During each of these floods, water from the river spilled into the wetlands in approximately equal amounts after passing through the adjacent bottomland forest.

Figure 1. Paired 1-ha experimental wetlands at the Olentangy River Wetland Research Park.

Macrophyte cover , species richness, and community diversity

Macrophyte coverage is estimated each year from aerial photography taken at the end of every growing season and coupled with ground truth surveys. Maps for each year are normalized to the same size basin map. Species richness is estimated through surveys conducted through the summer and fall. Macrophyte Community Diversity Index (CDI) is determined using relative areas of macrophyte community cover from the maps and using the mathematics of the Shannon-Weaver diversity index, with area instead of number of individuals of each species used.

Indices of Ecosystem Function

We use sixteen indicators to estimate ecosystem function of wetlands (Table 1). We are using one index of macrophyte function (net aboveground primary productivity), two indices of water column development, six indicators of wetland biogeochemistry, three indicators of nutrient retention, two indicators of benthic community development, and two indicators of avian community development. Our criteria for choosing these indicators are that they (1) are relatively easy to measure so that they can be repeated from year to year and (2) provide actual indicators of ecosystem function.

Macrophyte productivity

Net aboveground primary productivity (NAPP) has been estimated since 1997 through harvesting of 16 randomly selected plots in 21 possible locations in each basin. All aboveground biomass is harvested and weighed. Subsamples are taken to the lab and dried in a drying oven until constant weight to estimate dry/wet ratios.

Algal sampling and water column productivity

Algae are sampled several times each year in several locations in both wetlands with a plankton net tossed 5 m and retrieved with a cord. Samples representative of metaphyton such as attached and benthic algae are taken by

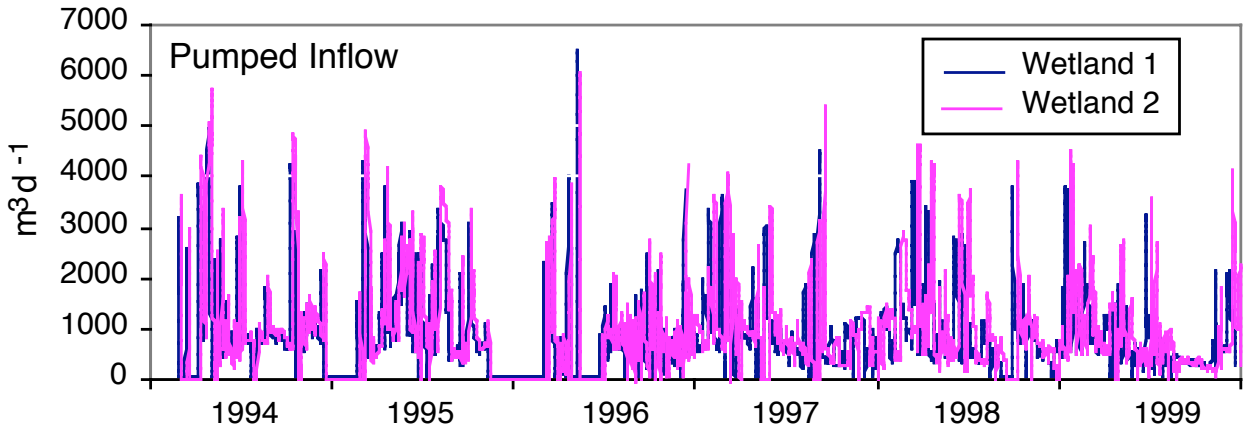

Figure 2. Pumped inflow to the two experimental wetlands for the initial 6 years, 1994-99.

hand. Algal species are identified by microscope at 100x and 400x and relative abundance of each genus is estimated. Daily dawn-dusk readings of dissolved oxygen at the outflows are used to estimate volumetric metabolism of the water column. Respiration is estimated as the average rate of oxygen decrease from dusk to dawn during two consecutive nights. Daytime net primary productivity estimated from the increase in dissolved oxygen between these two nights and corrected for daytime respiration, is used to estimate gross primary productivity of the water column.

Benthic invertebrates

Benthic invertebrates are sampled in late October –early November annually with Hester-Dendy plates (11 cm^2) at nine stations in each wetland. Sometimes this sampling is supplemented with dip net collections and bottle collections. Invertebrates are then sorted to lowest recognizable taxa . Shannon-Weaver diversity indices are estimated with these taxa count. Students t-tests are used to determine statistical differences between the two basins (α=0.05).

Water analysis

Water temperature, dissolved oxygen, pH, conductivity, and redox are measured twice-per-day (dawn and dusk) with Hydrolab H20G or YSI 6000 water quality sondes at the inflow and outflows of both wetland basins. Water samples are taken dawn and dusk each day at wetland inflow and outflows for turbidity analyses in the laboratory with a Hach ratio turbidimeter. Weekly water samples are

Table 1. Indicators of ecosystem function used to compare planted and unplanted experimental wetlands at Olentangy River Wetland Research Park, 1994-99.

Indicator of Ecosystem Function	Ecosystem Function
I. macrophyte community function	
1. net aboveground primary productivity	macrophyte community organic production
II. aquatic community development	
2. algal species richness	water column diversity
3. aquatic metabolism	water column organic production
4. benthic invertebrate diversity	aquatic community diversity
5. “clean water” species richness	balance of P and R
III. biogeochemistry	
6. temperature	shading of water column (due to vegetation)
7. turbidity	sedimentation (caused by plants/hydrology)
8. dissolved oxygen	oxidation/reduction (function of carbon dynamics)
9. pH	carbon uptake/release in water column
10. specific conductance	chemical precipitation/absorption
11. redox	oxidation/reduction balance
IV. nutrient dynamics	
12. total phosphorus	phosphorus retention
13. soluble reactive phosphorus	inorganic nutrient uptake
14. nitrate+nitrite	denitrification/nitrogen retention
V. avian use	
15. abundance	insect/aquatic community production
16. species richness	food source richness

taken at inflows and outflows of the wetlands for nutrients. These samples are split into filtered (0.45 μm) and unfiltered samples, frozen until analysis, and analyzed for total phosphorus, soluble reactive phosphorus, and nitrate-nitrogen (APHA, 1989; USEPA, 1983). Both total phosphorus and soluble reactive phosphorus methods employ the ascorbic acid and a molybdate color reagent method with a Lachat QuikChem IV automated system. Total phosphorus samples are first digested by adding 0.5 ml of 5.6 N H2SO4 and 0.2 g (NH4)2S2O8 to 25 ml of sample and exposing the samples to a heated and pressurized environment for 20 minutes in an autoclave. Nitrate + nitrate was measured with an Orion ion selective electrode until 1996 after which the Lachat system has been used with the cadmium reduction method.

Avian and Animal Use

The site was surveyed for birds from October 1992 through September 1996 on standard walking paths. The site was visited for these surveys 41 times over a 47-month period. Comparison of avian use of the basins resumed in 1999 through frequent visits to the basins in spring. Birds were noted by songs and by site. Muskrat use was estimated for the basins in the 1999-2000 winter by counting and measuring muskrat lodges. Ten minnow traps were deployed from the boardwalk in each wetland in spring 2000 and sampled daily to estimate fish, reptile, and amphibian activity.

Results and Discussion

Macrophyte Cover and Biodiversity

After an initial period of algal (mostly metaphyton) cover in the first two growing season (Wu and Mitsch, 1998), emergent macrophytes developed to where almost all of the available shallow water areas in both wetlands were vegetated by the end of the third growing season (Table 2; Figure 3). For years two and three, vegetation cover in the planted wetland rose from 13% to 36%; coverage in the unplanted wetland remained negligible in the second year (~0%) but increased dramatically in the third year to almost equal the planted wetland at 35%. By the end of the third year, the two wetlands had converged in vegetation cover, with both dominated by sedge communities dominated by *Schoenoplectus tabertaemontani* (a.k.a. *Scirpus validus*). By the end of the fourth year (1997), plant coverage in the unplanted wetland (W2) slightly exceeded that in the planted wetland (W1) (65% versus 60%). Plants in both wetlands continued to be dominated by *Schoenoplectus tabernaemontani*, with invasive *Typha* spp. now found in 5% and 17% respectively in W1 and W2 in 1997. During the last two years, vegetation cover reached 61 to 63% in W1 and 70 and 66 % in W2 for 1998 and 1999, respectively. By 1999, there were 5 communities comprising the 63% cover in W1 and 2 communities comprising the 66% cover in W2 (Table 2).

Macrophyte species richness increased dramatically in the middle years 1996 and 1997 and is now essentially identical in the two wetlands after 6 years (Figure 4a). By year 4, the number of macrophyte species in each wetland had reached 95 to 85 species respectively in W1 and W2; since then the two wetlands achieved almost the same number of species in 1999 (98 vs. 96 in W1 and W2 respectively). Most (8 of 13) of the introduced species are still found in the planted wetland W1 six years after the planting. Only 2 of these introduced plants are found in the naturally colonizing W2. In 1999, nine species are unique to W1 while 7 species are unique to W2. The basins are essentially identical when using plant richness as an indicator.

When the wetlands are viewed in terms of evenness of plant cover using our index of community diversity index (CDI), a dramatically different conclusion about macrophyte biodiversity is reached (Figure 4b). The wetlands diverged in community diversity first in 1995 when communities were first developing in the planted W1 but were nonexistent in the unplanted W2. Then the patterns of community diversity converged for two years and began to diverge in

Table 2. Dominant vegetation communities and other habitat and their percent cover in the two experimental wetlands at theOlentangy River Wetland Research Park, 1994-99. Numbers of percent of wetland basin.

Zones that are dominated by	1994		1995		1996		1997		1998		1999	
	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2
Open water	16.3	29.6	87.0	100	59.9	63.4	40.2	35.0	39.2	29.6	36.8	33.6
Algal mat	83.7	70.4										
Macrophyte Communities												
Schoenoplectus tabernaemontani			13.0	0.0	36.0	34.8	46.6	48.0	41.2	26.9	21.5	10.1
Typha spp.					4.1	1.9	5.0	16.6	1.1	43.5	8.9	56.3
Scirpus fluviatilis							2.3		4.4		2.9	
Nelumbo lutea							1.2	0.4	1.0	0.0		
Sparganium eurycarpum							4.7		13.1		25.4	
Sagittaria latifolia							0.1					
Spartina pectinata											4.5	
Total	100	100	100	100	100	100	100	100	100	100	100	100

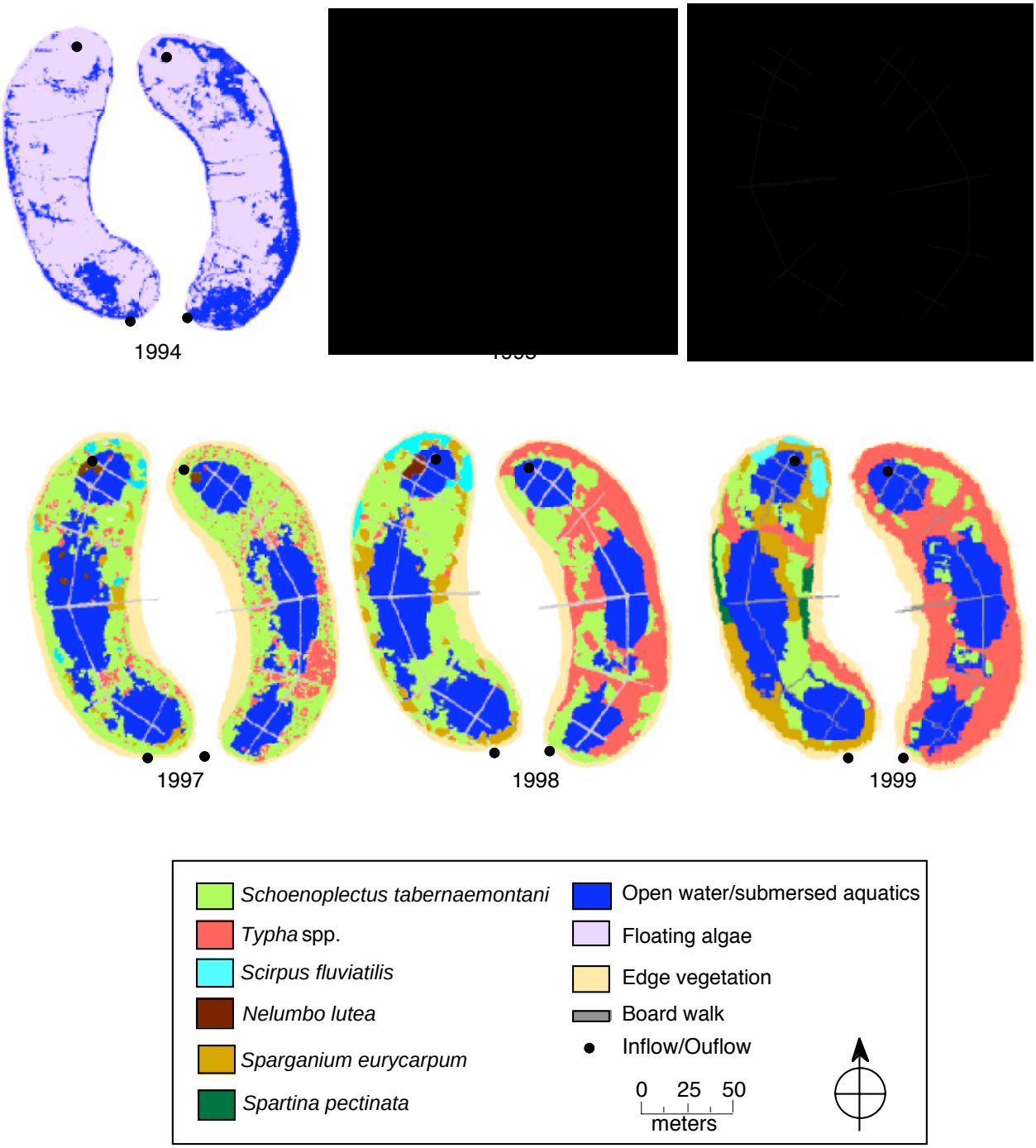

Figure 3. Comparison of major macrophyte and other aquatic communities in the two experimental wetlands, 1994-99.

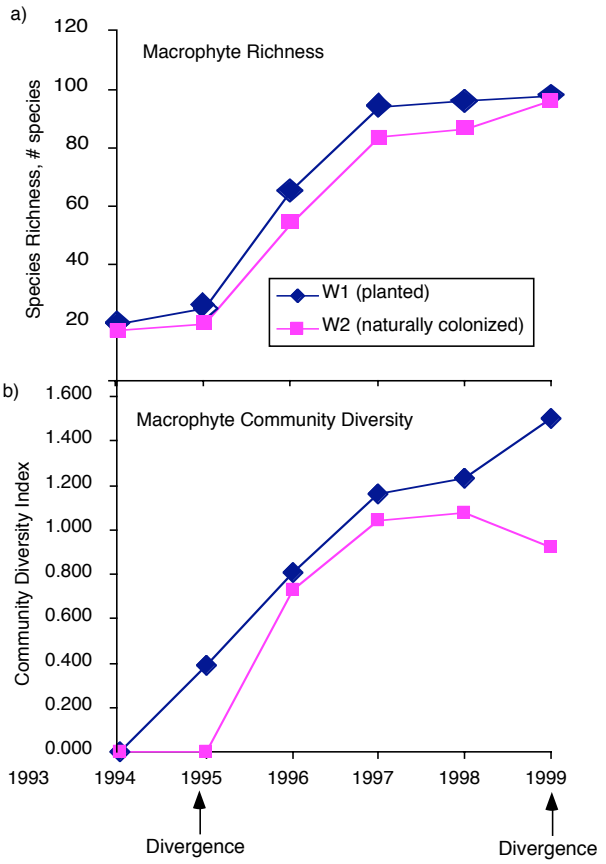

Figure 4. Comparison of a) macrophyte species richness and b) macrophyte community diversity index (CDI) of the two experimental wetlands, 1994-99. Note divergence of macrophyte community diversity (CDI) in 1995 (year 2) and in 1999 (year 6).

1998, the fifth year. By the sixth year, there was a second clear divergence in the CDI, with much greater value for the planted wetland than the naturally colonizing wetland. In essence, by the sixth year we have a pair of wetlands that had developed significantly different spatial diversity with no intervention by humans since the planting of one wetland in 1994. The stage is set to determine if function was different in the two wetlands in that year.

Typha spp., a clonal dominant that was not introduced during the 1994 planting, invaded both wetlands during the first year but began to colonize the unplanted W2 at a rapid rate, beginning in the fourth year (Figure 5). It began to dominate W2 in the fifth year (1998) when it was 43% of the wetland area and the sixth year (1999) when the cover increased to 56%. It expanded much more slowly in the same years in the planted wetland, going from 1% to 9% cover. The rapid invasion of this plant into the W2, with a much slower invasion into W1 because of competition with planted species, is the primary reason that the CDI shown in Figure 4b is different for the two wetlands in 1999.

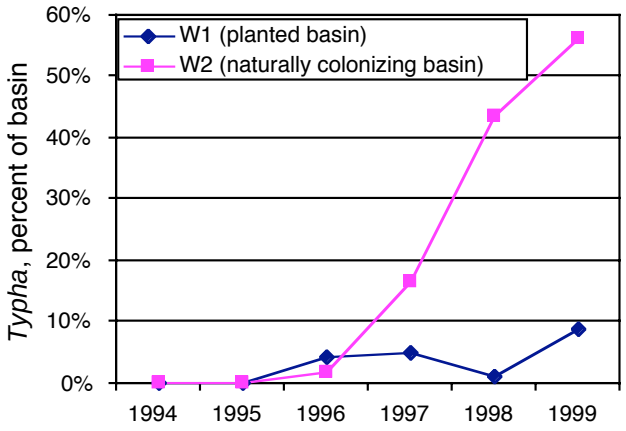

Figure 5. Percentage of *Typha* spp. cover from 1996-99 in the two experimental wetlands.

Ecosystem Function Indicators

The sixteen indicators described in Table 1 have been compared between the two basins for the six years of this study and are discussed here.

Macrophyte Community Function

Macrophyte net aboveground primary productivity (NAPP) was similar in the fourth year in the two basins, but became statistically higher in the unplanted low diversity wetland (W2) in both years 5 and 6 by 55 and 56% respectively over W1 (Figure 6a). The high community diversity in W1 did not cause higher NAPP in that basin. In fact, quite the opposite happened. The productive monoculture of *Typha* had far greater productivity than did any of the diverse plant communities in W1.

Aquatic Community Development

Algal growth, primarily as dense benthic and floating metaphyton, has been significant in both wetlands throughout the study period, particularly in the first year, when large metaphyton mats were composed of *Hydrodictyon reticulatum* (L) Lag. and *Rhizoclonium* spp. along with extensive epiphytes of several species of Chlorophyta and Chrysophyta. In the second and third years, algal productivity continued with less *Hydrodictyon* and more *Cladophora*, *Spirogyra* and *Rhizoclonium*. In the second year, the planted wetland (W1) carried an average of 80% of all of the genera identified while the unplanted wetland (W2) supported 70% of those genera. In the third year (1996), the same statistic was 79% for W1 and 74% for W2, illustrating some convergence. An apparent increase in algal diversity in W2 in the third year correlates with the introduction of macrophyte cover. Macrophytes may be increasing microhabitats for the microphytes since over 130 genera were identified in the two wetlands by the end of three years. By 1998, the deepwater areas in the two wetlands started to become dominated by *Lemna minor*, causing dramatic decreases in metaphyton during some periods. Although

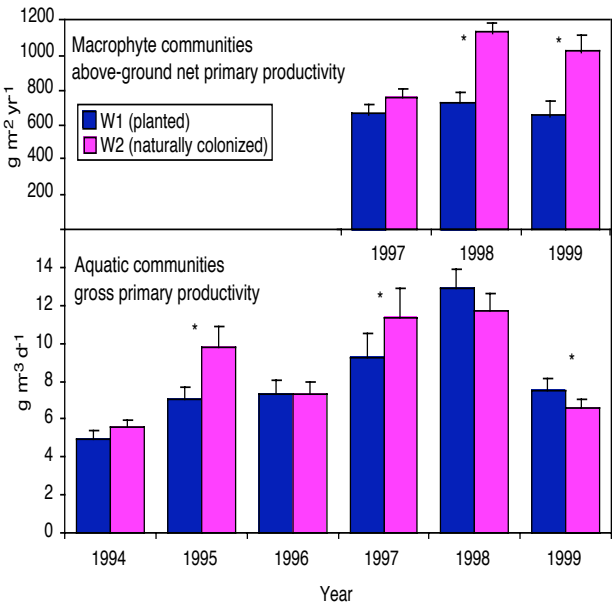

Figure 6. a) Macrophyte net aboveground primary productivity (NAPP), and b) aquatic community primary productivity of two experimental wetlands. Asterisk (*) indicates significant difference between wetlands (a = 0.05). Macrophyte NAPP was not estimated during the first 3 years through harvesting methods. But it was different in 1995 because there were essentially no macrophyte communities in W2 in 1995.

there have been some differences in the two basins in 1998 and 1999, it appears that there has been general convergence of algal species since year 3 (1996).

Gross primary productivity in the water column, as a functional measure of the algae, was inversely related to macrophyte NPP and cover (Figure 6b). When biomass of macrophytes was nonexistent or similar in the two wetland basins, as was the case in the first (1994) and third (1995) years, GPP in the water column was similar in both wetlands. When there was considerable macrophytes in the planted wetland but not in the unplanted wetland (W2) in the second year , GPP was higher in the unplanted wetland W2 by 38% (Figure 6b). The same situation was seen in 1997 with higher GPP in W2. The situation reversed in 1999 when statistically higher water column productivity occurred in the planted wetland (W1) than in the naturally colonizing wetland (W2). This is consistent with the much greater macrophyte biomass in W2 which shades the water more and even causes slightly lower water temperatures (see below) in W2. Both lower light and water temperatures could decrease GPP in the water column.

Diversity measurements of the benthic invertebrate community has been used as an indicator of aquatic biota function for the wetlands (Table 3). In the first year, the diversity and number of taxa observed were generally similar. In the second year, there were more aquatic taxa observed in the unplanted W2 (20 taxa) which was essentially devoid of emergent plants than in the planted W1 (18 taxa). Aquatic species richness was higher in W1 (38 taxa) than in W2 (32 taxa) in the third year but diversity indices were similar. Invertebrate diversity was statistically similar in 1997 and 1998 but were statistically different in 1999 when an overall greater invertebrate diversity in the Typha-dominated W2. The wetland with low macrophyte diversity had the higher invertebrate diversity. Except for the first two years of wetland development, the clean water species richness appears to be similar in both wetlands.

Biogeochemistry

Water chemistry changes as the water flows through the wetlands indicate several ecosystem functions in our wetlands (Table 1; Figure 7). Temperature increases through the wetlands continue to decrease each year as the biomass of the macrophytes shade the water. Differences between the two basins were significant in 1999 with statistically cooler water discharging from W1. Dissolved oxygen was higher in the planted W1 in 1999 when there was more light reaching the water column because of substantially less macrophyte biomass.

The pH has been significantly different between the two wetlands in four of the six years. It increased more in W2 in the early years (1994 and 1995). This pattern reversed where the planted W1 had significantly greater pH than the

Table 3. Benthic invertebrate diversity in two experimental wetlands.

Year	Total count diversity index		"Clean water" diversity index	
	W1	W2	W1	W2
1994 (planting)	0.63	0.69	0.45	0.60
1995 (divergence)	0.50	0.62	0.98	0.51
1996 (convergence)	0.88	0.83	0.88	0.86
1997 (convergence)	1.34 ± 0.02	1.41 ± 0.18	1.23 ± 0.28	0.96 ± 0.17
1998 (convergence)	0.58 ± 0.43	0.82 ± 0.56	0.58 ± 0.43	0.73 ± 0.45
1999 (divergence)	**0.63 ± 0.05***	**0.91 ± 0.12***	0.49 ± 0.13	0.61 ± 0.17

W1 = planted wetland; W2 = natually colonizing wetland
"Clean water" = all taxa except chironomids, oligochaetes, and tubificids
Indices are Shannon-Weaver index
*Significant differences (α = 0.10, n=3) between wetlands

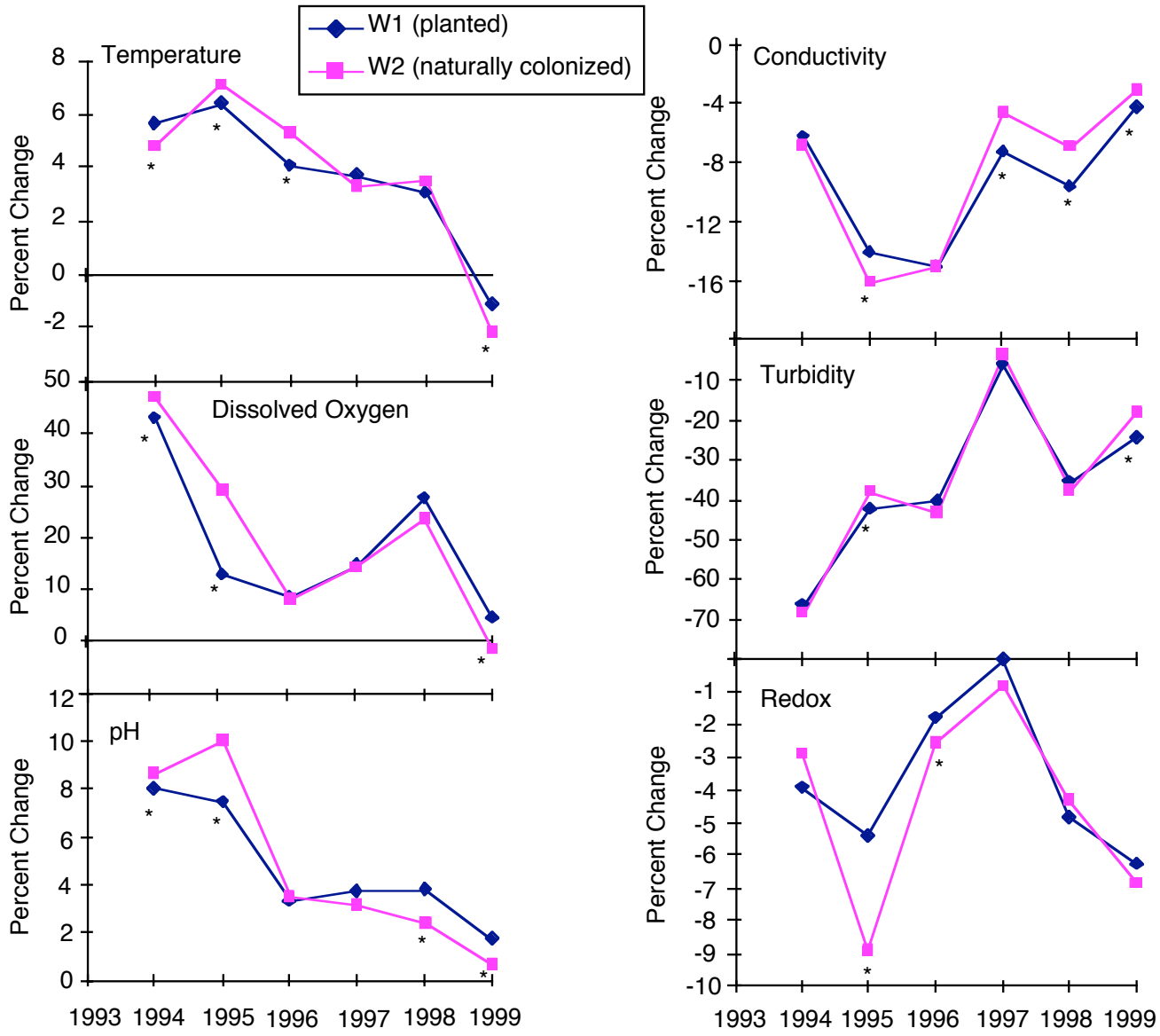

Figure 7. Water quality changes through experimental wetlands for 1994-99: a) temperature; b) dissolved oxygen; c) pH; d) conductivity; e) turbidity; f) redox potential. Asterisk (*) indicates significant difference between wetlands ($\alpha = 0.05$).

unplanted wetland in 1998 and 1999. Conductivity changes have been significantly different between the two wetlands in the second year and in the final 3 years. Conductivity decreased more in the naturally colonizing W2 in 1995, possibly because there was more precipitation of calcium carbonate and related minerals because of no shading by plants; then the pattern switched, with conductivity decreasing significantly more in the planted wetland W1, presumably because it then had less biomass shading the water. Higher temperature, pH and dissolved oxygen and lower conductivity in W1 in 1999 are consistent with higher algal productivity and lower macrophyte biomass in this wetland in 1999. Algal photosynthesis leads to higher dissolved oxygen; it also leads to higher pH by depleting free CO_2 and shifting the carbonate equilibrium; higher pH in turn leads to a greater precipitation of dissolved ions, thereby decreasing the conductivity.

Turbidity (general measure of suspended solids) followed a general pattern of significant differences in the second and sixth years, the general years in which the macrophyte CDI was different. In 1999, the sixth year, turbidity was significantly lower in the planted W1, Turbidity decreased less in the wetland that now had the higher macrophyte productivity, possibly suggesting a higher export of particulate carbon from that wetland. Redox potential has not differed between the two wetlands except early in the study. Overall, water chemistry changes indicative of biological function are different for 5 of the 6 chemistry indicators in 1999, supporting the contention that the wetlands are functionally different in 1999. Only in 1995, when all 6 parameters were different, was a higher difference seen.

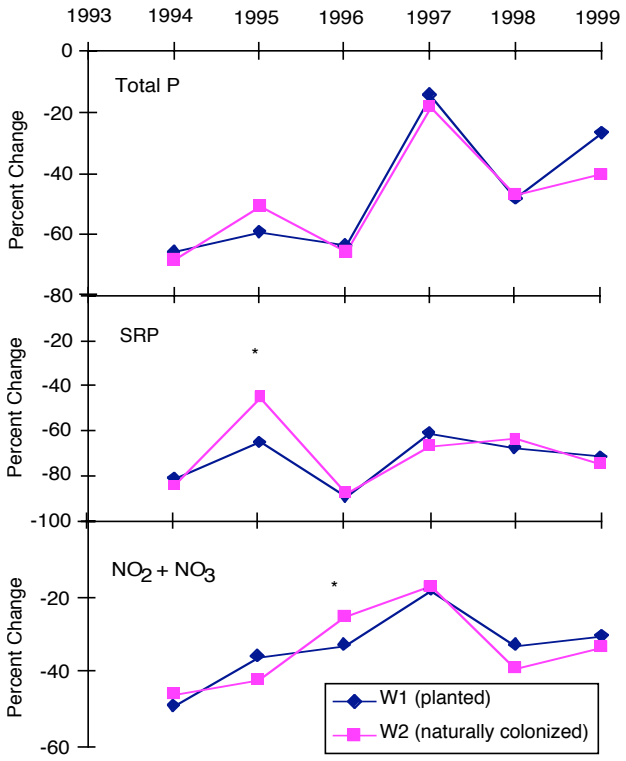

Figure 8. Nutrient changes through experimental wetlands for 1994-99: a) total phosphorus; b) soluble reactive phosphorus; c) nitrite + nitrate nitrogen. Asterisk (*) indicates significant difference between wetlands (α = 0.05).

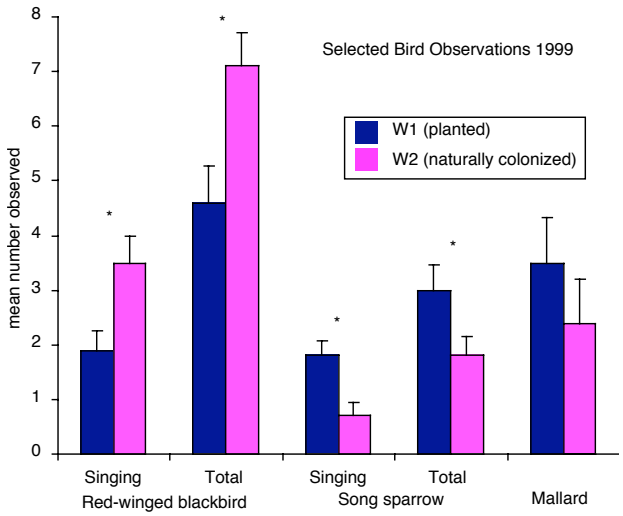

Figure 9. Bird observations comparing the two experimental wetlands in 1999. Asterisk (*) indicates significant difference between wetlands (α = 0.05).

Nutrient Retention

Nutrient (phosphorus and nitrogen) reduction continues to be significant in both wetlands throughout the six years (Figure 7) but few statistically significant differences between the wetlands have been noted over the six-year study. Total phosphorus concentration reductions have ranged from 18 to 73% per wetland but the two wetlands have not been significanly different through the six years of measurements. Percent reduction sof soluble reactive phosphorus (SRP) has been higher (50 to 90% removal) than that of total phosphorus and have been consistent from year to year. Only in the second year was SRP retention different between the two basins. Percent reductions of nitrate+nitrite-nitrogen have remained consistent from year to year (generally between 30 and 60% reduction in each wetland and only differed between the wetlands once. A significant difference (a = 0.05) was seen between the two wetlands only in the third year when the planted W1 retained more nitrogen.

Avian Use

A total of 150 bird species have been found in the study area from 1992-99 with a 20% increase in species richness in the first year of wetland construction, another 8% increase during the second year, and an additional 5% increase in the third year. The creation of the wetlands resulted in the addition of about 35 wetland-specific bird species to the site overall. Because of the proximity of the two wetlands, it has been generally difficult to compare avian use of the two wetlands. Nevertheless, surveys in the second year found that wetland birds demonstrated a marked preference for the planted W1 as this wetland consistently supported a greater number of species (nesting and migratory) and total individuals than did the unplanted W2. Two species in particular, the sora (*Porzana carolina*) and marsh wren (*Cistothorus palustris*), were found exclusively in the planted wetland in the second year. By the third year, with the development of vegetation cover in the unplanted W2, differential bird use between the two wetlands declined and similar numbers and richness of species were found in each. But with the development of different macrophyte communities in 1998 and 1999 in the two wetlands, more recent differences in bird use have been observed (Figure 9). There were significantly greater numbers of red-winged blackbirds (*Agelaius phoeniceus*) in W2 and significantly greater numbers of song sparrows (*Melospiza melodia*) in W1. Mallards (*Anas platyrhynchos*) and other ducks, while appearing to be more plentiful in W2 in 1999, were not significantly different in numbers between the two basins.

Overall changes in Wetland Function

Using our indicators of wetland function, there have been two occasions where the two wetlands were dissimilar in function (Figure 10; Table 4) The second year after wetland construction (1995), substantial macrophyte cover had developed only in the planted wetland W1 as expected and none was present in W2. A noticeable increase in algal aquatic productivity and different algal communities in W2, combined with more macrophytes in the planted W1, caused different water chemistry, some differences in the

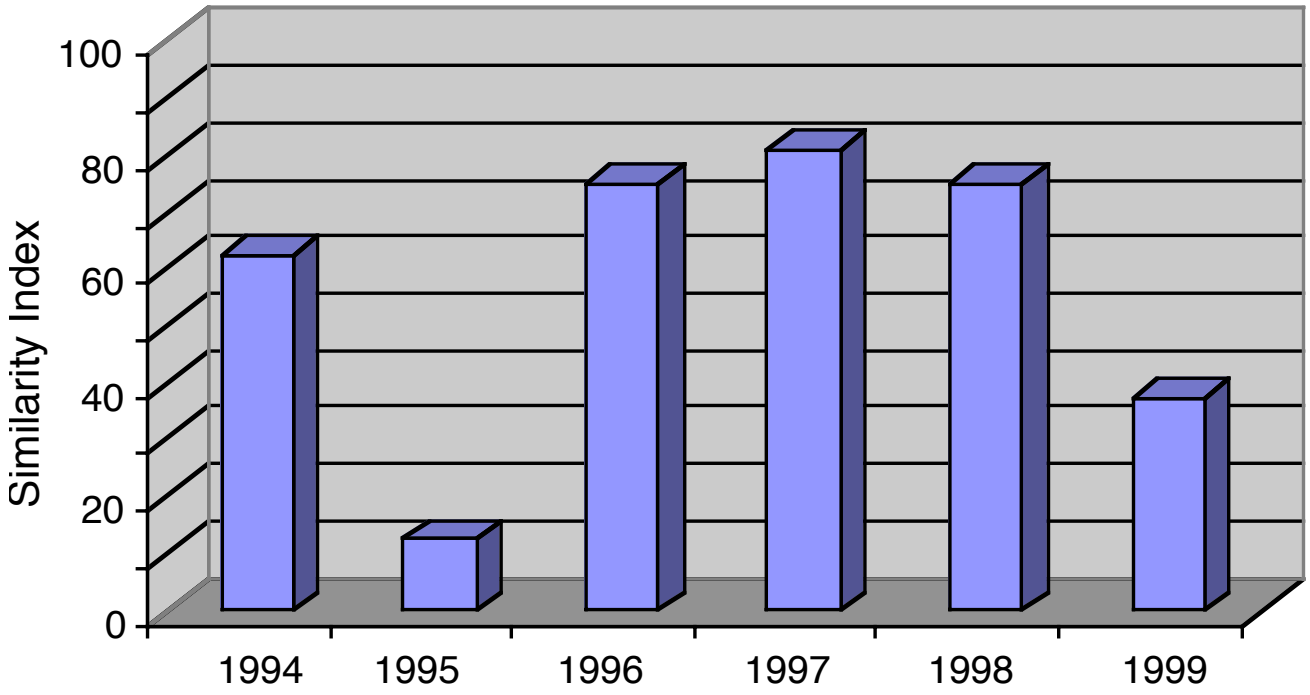

Figure 10. Summary of similarity index between the two experimental wetlands for 1994-99. This similarity index is based on the 16 indicators listed in Table 1.

Table 4. Summary of indices comparing Wetland 1 (W1) and Wetland 2 (W2) for 6 years, 1994-99.

Macrophyte Diversity, CDI	1994 W1=W2	1995 W1>W2	1996 W1=W2	1997 W1=W2	1998 W1=W2	1999 W1>W2
I. Macrophyte Community Function						
NAPP	W1=W2	W1>W2	W1=W2	W1=W2	W1<W2	W1<W2
II. Aquatic Community Development						
Algal species richness	W1=W2	W1>W2	W1>W2	W1=W2	W1=W2	W1=W2
Aquatic metabolism	W1=W2	W1<W2	W1=W2	W1<W2	W1=W2	W1>W2
Benthic invertebrate diversity	W1=W2	W1<W2	W1=W2	W1=W2	W1=W2	W1<W2
Clean Water species richness	W1<W2	W1>W2	W1=W2	W1=W2	W1=W2	W1=W2
III. Biogeochemistry						
Temperature	W1>W2	W1<W2	W1<W2	W1=W2	W1=W2	W1>W2
Turbidity	W1=W2	W1<W2	W1=W2	W1=W2	W1=W2	W1<W2
Dissolved Oxygen	W1<W2	W1<W2	W1=W2	W1=W2	W1=W2	W1>W2
pH	W1<W2	W1<W2	W1=W2	W1=W2	W1>W2	W1>W2
conductivity	W1=W2	W1>W2	W1=W2	W1>W2	W1<W2	W1<W2
redox	W1=W2	W1>W2	W1>W2	W1=W2	W1=W2	W1=W2
IV. Nutrient Dynamics						
Total P	W1<W2	W1=W2	W1=W2	W1=W2	W1=W2	W1=W2
SRP	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2	W1=W2
NO_3+NO_2	W1=W2	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2
V. Avian Use						
Bird abundance	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2	W1<W2
Bird species richness	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2	W1=W2

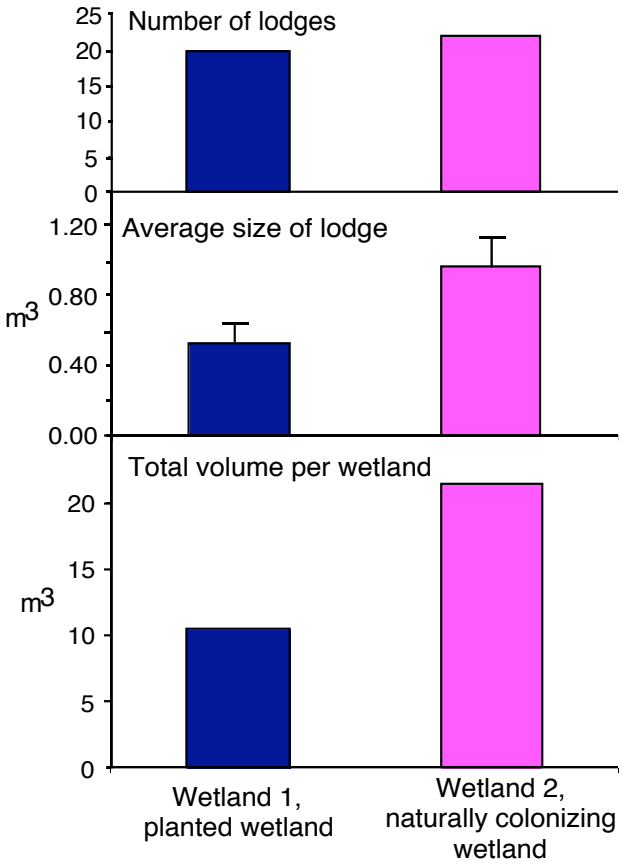

Figure 11. Muskrat activity in the two experimental wetlands in winter of 1999-2000 indicating a) total number of muskrat lodges in each basin; b) average volume of lodges in each wetland; c) total volume of lodges in two wetlands. This is a general indication of the potential winter population of muskrats in each wetland.

aquatic community diversity, and differential bird use. Only 13% of the ecosystem function indicators in Table 4 were similar. In years 3, 4, and 5, the wetlands had converged with 75 to 88% of the indicators similar. But the similarity in function dropped to 44% in year six (1999) as the macrophyte community diversity diverged between the two wetlands. The two basins were once again different, this time possibly due to the differences in plant communities (Figures 3 and 4b). It cannot be proven, but the apparent differences in macrophyte biodiversity probably led to changes in ecosystem function in 1999 after years of relative similarity in function between the wetlands.

Animal Use

The divergence of the two wetlands in 1999 is supported by two other pieces of evidence collected in early 2000. The size and volume of muskrat lodge are being used as indicators of muskrat populations and activity. Muskrat lodges, while similar in numbers in the winter of 1999-2000 between the two basins, were significantly bigger in W2 than W1, purportedly because of higher macrophyte productivity, especially by *Typha*, in W2. When the total "volume" of all the muskrat lodges is estimated, there is room for almost twice as many muskrats in W2, the naturally colonizing wetland, than in the planted wetland (Figure 11).

Table 5. Comparison of amphibians, reptiles, and fish caught in 20 traps in two wetlands in spring of 2000. Numbers are organism caught per trap-day.

Species	Wetland 1 (mean ± S.E.)	Wetland 2 (mean ± S.E.)
Rana catesbeiana	0.0147 ± 0.0062	0.138 ± 0.0236*
Rana pipiens	0.0324 ± 0.0092	0.0224 ± 0.0088
Nerodia sipedon	0.0059 ± 0.0041	0.023 ± 0.0079*
Lepomis sp.	21.4 ± 1.95	34.1 ± 2.62*

* indicates significantly higher number compared to Wetland 1 ($\alpha = 0.05$)

There were also statistically higher numbers of *Rana catesbeiana* (bullfrog tadpoles), *Nerodia sipedon* (norther water snakes) and *Lepomis* sp. (mostly green sunfish) in the natually colonizing W2 than in the planted W1 in the early 2000 sampling, again reflecting the greater primary productivity of macrophytes in this wetland (Table 5). In effect, the higher productivity in W2 is being translated into higher secondary productivity of many other parts of the ecosystem compared to the lower productivity in the planted W1.

Conclusions

Our long-term experiment , while only 6 years old, demonstrated several important points applicable to restoration and creation of wetlands as well as other ecosystems.

1. Planting does have a profound effect on ecosystem function of created wetlands, even several years after the planting. But we also conclude that some of the effects of planting are desirable; some are not. The two wetlands, with initial conditions essentially identical except for plant introduction, experienced two periods of functional divergence when the introduction of species may have had a temporary effect on ecosystem function. We conclude that both periods of divergence were connected to the original planting. Functional differences, though not dramatic, were seen in aquatic productivity, water quality, habitat value, and aquatic diversity when the wetlands diverged these two times.

2. The addition of species to enhance biodiversity in wetland creation actually can lead to lower productivity of macrophytes and subsequently other parts of the wetland ecosystem. After 6 years, NAPP was higher by 50%, invertebrate diversity was higher, and amphibian, reptile, fish, and mammal use was greater in the naturally colonizing wetland. Other studies on smaller replicated plots where plant diversity was artificially maintained (e.g., Naeem et al., 1994; Tilman et al, 1996, 1997; Naeem and Li, 1997) have suggested higher productivity and "more desirable" ecosystem function with biodiverse vegetation. Our study

does not support that contention. Biodiversity does not necessarily enhance "desirable" ecosystem functions. But introduced species do change ecosystem function.

3. The continual introduction of plant, animal, and microbial species through water flows, atmospheric transport, and biological vectors give self-design a significant opportunity to manifest itself in created wetlands if they are opened to such flows, regardless of whether propagules are introduced by humans. Self-design is the property of ecosystem development in which the chance presence of species is analogous to the occasional mutation necessary for evolution to proceed. Self-design in ecosystem restoration and creation is enhanced if an ecosystem is open to allow seeding, through human or natural means, of enough species' propagules; the system itself will optimize its design by selecting for that assemblage of plants, microbes, and animals best adapted for existing conditions. This study underscores the importance of self design as an operating approach when creating and restoring ecosystems.

4. Whole ecosystem studies, when conducted over a long period, can provide useful comparisons of ecosystem functions, even when replication is not possible due to the large size of these systems. Size of the ecosystem compensates for the lack of replication.

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